

RELATIONSHIP BETWEEN CANOPY DYNAMICS AND STEM VOLUME PRODUCTION OF FOUR SPECIES RECEIVING IRRIGATION AND FERTILIZATION

Christopher B. Allen, Rodney E. Will, Terry Sarigumba, Marshall A. Jacobson,
Richard F. Daniels, Stephen A. Kennerly¹

Abstract—We measured the effects of irrigation and varying levels of fertilization on intercepted photosynthetically active radiation (IPAR), projected leaf area index (LAI), and foliar nitrogen concentration ([N]) in order to determine the relationship between resource availability, canopy size, and stem-volume growth. Stands of sycamore (*Platanus occidentalis* L.), sweetgum (*Liquidambar styraciflua* L.), loblolly pine (*Pinus taeda* L.), and slash pine (*Pinus elliottii* Engelm.) planted in 1997 near Mount Pleasant, GA, received five treatments: control, irrigation only, and irrigation with 57, 85, and 114 kg N ha⁻¹ year⁻¹. Beginning in March 2001, sampling for foliar [N], IPAR, and leaf litter were conducted approximately every 6 weeks. Irrigation and fertilization increased stem-volume growth during the 2001 growing season. Annual IPAR and LAI were well correlated with stem-volume growth ($r^2 = 0.80$, $r^2 = 0.75$, respectively—averages of four species). Foliar [N] and stem-volume growth were significantly correlated for sweetgum ($r^2 = 0.76$) and sycamore ($r^2 = 0.80$). These results indicate that IPAR is the best predictor and may be the primary driver of stem-volume growth.

INTRODUCTION

The positive impact of fertilization on site productivity depends on nutrient application rates and frequency, genotypic variation (within and between species), inherent site factors (e.g., climate, soil factors, relief, etc.), and complementary cultural treatments (e.g., site preparation, weed control, thinning, etc.). Whereas growth enhancements are well documented (Fife and Nambiar 1997, Lockaby and others 1997, Maier 2001), the reasons for increased growth are less evident. Several factors related to canopy dynamics have been identified as potential drivers of growth accelerations; some are fertilization, including increased foliage development for light interception and photosynthetic surface area (Albaugh and others 1998, Beets and Whitehead 1996, Samuelson 1998), increased photosynthetic capacity (Murthy and others 1996, Samuelson 2000), and increased partitioning of fixed carbon to aboveground biomass (Albaugh and others 1998, Gower and others 1992, Keyes and Grier 1981). A better understanding of the mechanisms driving growth hopefully will permit better management regimes and increase the precision of growth predictions using process-based models, such as 3-PG, MAESTRO, and BIOMASS.

Nitrogen fertilization usually increases foliage development (Kuers and Steinbeck 1998, Sampson and Allen 1998). This has a positive impact on growth by increasing surface area for carbon fixation and by increasing the amount of radiation intercepted by the stand. Although photosynthetic surface area and radiation interception are both mediated by foliage development, their relationship differs between stands or with stand development due to differences in foliage display. Nitrogen fertilization also often increases foliar nitrogen concentration (Beets and Whitehead 1996; Jose and others, in press; Maier 2001; Nelson and others 1995). This increase may correspond to subsequent

increases in photosynthetic capacity (McMurtrie and others 1990, Murthy and others 1996, Samuelson 2000). However, in some cases such as mature pine stands, higher foliar nitrogen concentrations do not stimulate photosynthesis (Maier and others 2002; Munger and others, in press).

Water availability, like fertilization, can have a large positive effect on stand growth, especially when water is limiting (Jose and others, in press; Li and Wang, in press; McMurtrie and others 1990; Samuelson 1998; Samuelson and others 2001). In other instances, irrigation had little impact on growth of forest stands (Albaugh and others 1998, Maier 2001). Water stress may (Li and Wang, in press; Osorio and others 1998; Wendler and Millard 1996) or may not (Albaugh and others 1998, Green and others 1994) decrease leaf-area development. Likewise, irrigation may dilute foliar nitrogen concentration (Jose and others, in press; Samuelson and others 2001) or may have no effect (Murthy and others 1996, Samuelson 1998).

The objectives of this study were to (1) determine how various levels of resource availability, as altered by irrigation and fertilization, impact leaf area index (LAI), intercepted photosynthetically active radiation (IPAR), and foliar nitrogen concentration ([N]) of four fast-growing tree species (*Pinus taeda* L., *Pinus elliottii* Engelm., *Liquidambar styraciflua* L., and *Platanus occidentalis* L.), and (2) relate the responses of LAI, IPAR and [N] to stem-volume growth.

METHODS

Study Description

The study site was located in the Lower Coastal Plain, near Mount Pleasant, GA, (31°23'N, 81°43'W). Soils were deep, acidic sands that previously supported a pine plantation. In 1997, loblolly pine, slash pine, sweetgum, and sycamore were planted in 0.10-ha plots at a density of 1,790 trees

¹ Graduate Student and Associate Professor, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602; Plum Creek Timber (retired), 202 Twin Lakes Drive, Brunswick, GA 31525; Manager, Forest Productivity, Plum Creek Timber Company, 22 North Main St., Watkinsville, GA 30677; Associate Professor, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602; and Silviculturalist, Southeastern Region, Plum Creek Timber Company, 200 County Road #216, Palatka FL 32177, respectively.

ha⁻¹ to test the effects of irrigation combined with increasing fertilization rates. The study was a randomized complete block design, with five treatments replicated over three blocks. The treatments were as follows (with treatment codes): control (C), 3.05 cm water week⁻¹ (I), 3.05 cm water week⁻¹ + 57 kg N ha⁻¹ year⁻¹ (I + N57), 3.05 cm water week⁻¹ + 85 kg N ha⁻¹ year⁻¹ (I + N85), and 3.05 cm water week⁻¹ + 114 kg N ha⁻¹ year⁻¹ (I + N114). Treatments were initiated during the first growing season. During the 2001 growing season, fertilizer was applied as 12-4-8 N-P-K with micro-nutrients.

Volume Estimation

Dormant season diameter at breast height (d.b.h.) and total height were measured annually on every tree. Stem-volume equations were calculated using taper measurements of 180 harvested trees (45 per species) at the end of the 2002 growing season. Three trees per plot were selected for harvest based on prior determinations of d.b.h. distribution (mean d.b.h., mean d.b.h. \pm standard deviation). Taper was calculated by measuring stem diameter at ground line, 1 m, d.b.h., 2 m, and every subsequent 2-m interval. A single taper equation was used for each species, as linear regression analysis showed no difference between treatments within a given species. Taper equations were used to calculate volume at the end of the 2000 and 2001 growing seasons using the annual measurements of height and diameter. Growth during the 2001 growing season was calculated as the difference in standing volume at the end of the 2001 and 2000 growing season. No mortality occurred during the 2001 growing season.

Intercepted Radiation

Measurements of IPAR were made under cloud-free conditions every 30 to 60 days during the 2001 growing season (six total measurements) with the Sunscan Canopy Analysis System (Delta-T Inc., UK). Percent IPAR per plot was calculated based on incident radiation and the average of 50 subsamples beneath the canopy ($IPAR = 1 - \text{canopy transmittance/incident radiation}$). As zenith angle has a large effect on radiation interception, IPAR was corrected to a standard angle of 30° with empirically derived equations. To derive these correction equations, hourly measurements were made in plots of each species and treatment combination during midsummer. From these measurements, regression equations were derived [$IPAR = a + b (\text{zenith angle})^2$] for each species treatment combination. Annual energy capture was calculated by interpolating percent IPAR between sampling dates, multiplying by average incoming radiation for each day, and then summing the daily totals. Solar energy data from the National Solar Radiation Database (Renewable Resource Data Center, U.S. Department of Energy) were used for daily incident radiation values. The most recent data available (1981-90) from Savannah, GA, (closest weather station) were averaged.

Leaf Area Index

Projected LAI was determined from litter biomass collected from five randomly placed litter traps per plot (trap area = 0.47 m²). Leaf litter was collected monthly after the initiation of leaf senescence (around October) and continued through mid-January. Pine litter also was collected several times during the growing season. Leaf litter was dried at

70 °C and weighed. Monthly biomass collection weights were summed and scaled to the hectare basis. Litter biomass was converted to LAI using estimates of specific leaf area (average of four growing-season measurements) and empirically derived factors to adjust for weight loss between fresh leaves and litter. For pines, all-sided LAI was converted to projected LAI by dividing by 3.14 (Grace 1987).

Foliar Nitrogen Concentration

Samples for foliar [N] were collected four times during the growing season using a shotgun. On each sampling date, three pine or four hardwood foliar samples were collected from the upper third of the canopy of each plot. Pine foliage was separated into the two age cohorts (when present), and several representative fascicles were collected from each flush. Samples were kept on ice until placed in an oven to dry at 70 °C. After drying, samples were ground to a fine powder with an 8000-D mixer mill (Spex Certiprep, Inc., Metuchen, NJ) and analyzed for [N] with a NA 1500 nitrogen/carbon analyzer (CE Elantech Inc., Lakewood, NJ, USA).

Statistical Analysis

Separate analyses were conducted to determine the effect of irrigation (C vs. I) and the effect of fertilization (I, I + N57, I + N85, I + N114). For standing volume, volume growth, annual energy capture, LAI, and average foliar [N], the effect of fertilization was determined with analysis of variance (ANOVA) whereas the effect of irrigation was analyzed with a Student's t-test. Linear regression analysis was used to correlate IPAR, LAI, and foliar [N] with stem-volume growth and included irrigated and non-irrigated plot data.

RESULTS

Volume

Fertilization in conjunction with irrigation increased standing stem volume when compared to irrigation alone. Although there were no significant differences between the three levels of fertilization, the I + N85 treatment consistently resulted in the highest standing volume, showing 57-percent, 69-percent, 514-percent, and 209-percent gains over the I treatment for slash pine, loblolly pine, sweetgum, and sycamore, respectively (fig. 1). Compared to the control, irrigation significantly increased standing volume only for hardwood species (sweetgum, 103 percent; sycamore, 340 percent) (fig. 1).

For the 2001 growing season, fertilization significantly increased volume growth for sweetgum and sycamore, with increases of 160 percent and 667 percent, respectively, for the I + N85 treatment compared to the I treatment (fig. 1). Although not statistically significant due to variation between blocks, loblolly pine and slash pine stem-volume growth increased by 52 percent and 65 percent, respectively, due to fertilization. Both hardwood species showed large increases in stem growth during the 2001 growing season due to irrigation (sweetgum, 343 percent; sycamore, 1980 percent).

Intercepted Radiation

Fertilization increased annual IPAR for loblolly pine, slash pine, sweetgum, and sycamore, with increases of 31, 40, 253, and 41 percent, respectively (fig. 2). In all cases, the

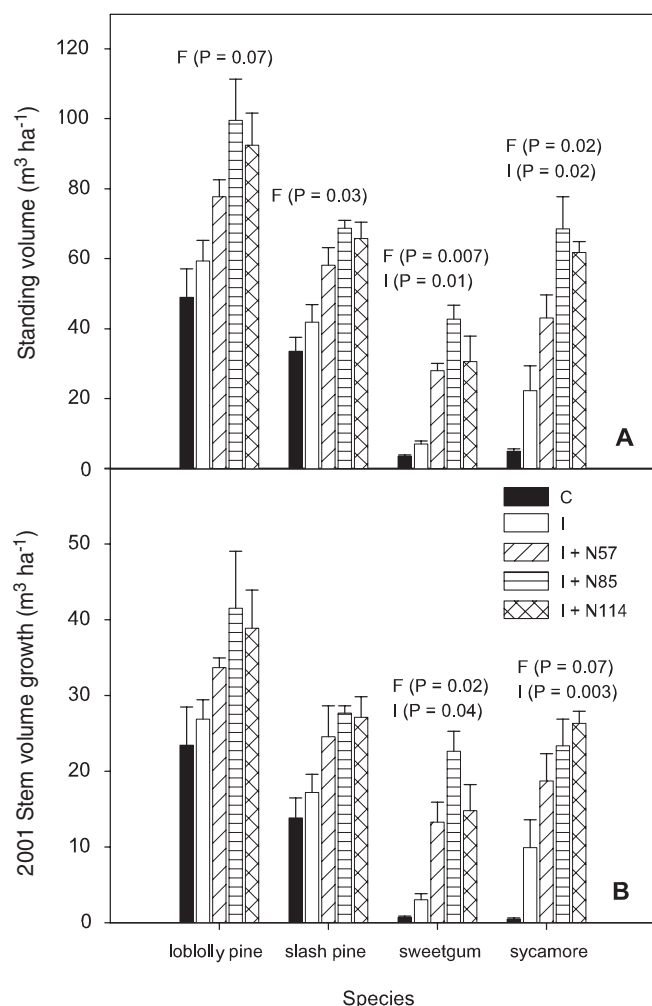


Figure 1—Standing volume at the end of the 2001 (fifth) growing season (A) and 2001 stem-volume growth (B). Treatment codes represent: C = control; I = 3.05 cm water week⁻¹; I + N57 = 3.05 cm water week⁻¹ + 57 kg N ha⁻¹ year⁻¹; I + N85 = 3.05 cm water week⁻¹ + 85 kg N ha⁻¹ year⁻¹; I + N114 = 3.05 cm water week⁻¹ + 114 kg N ha⁻¹ year⁻¹. F indicates a significant effect of fertilization, I indicates a significant effect of irrigation with P-values in parentheses (bars represent 1 standard error).

mid- and high-level fertilization treatments showed the largest enhancement, although differences were not significant among the three fertilization treatments. Irrigation caused large increases in the radiation interception of hardwood species, with sweetgum and sycamore showing 133 percent and 253 percent increases, respectively. Annual IPAR was highly correlated with stem-volume growth during the 2001 growing season for all species (fig. 3).

Leaf Area Index

Only the 2000 cohort of foliage (cohort on the tree for the entire 2001 growing season) was available for estimation of pine LAI; however, it was shown that fertilization increased LAI for both species of pine. Although differences among fertilization treatments were small, the I + N114 treatment resulted in the largest gain over the I treatment, with increases of 68 percent and 88 percent for loblolly and slash pine (fig. 2). Although fertilization did not significantly

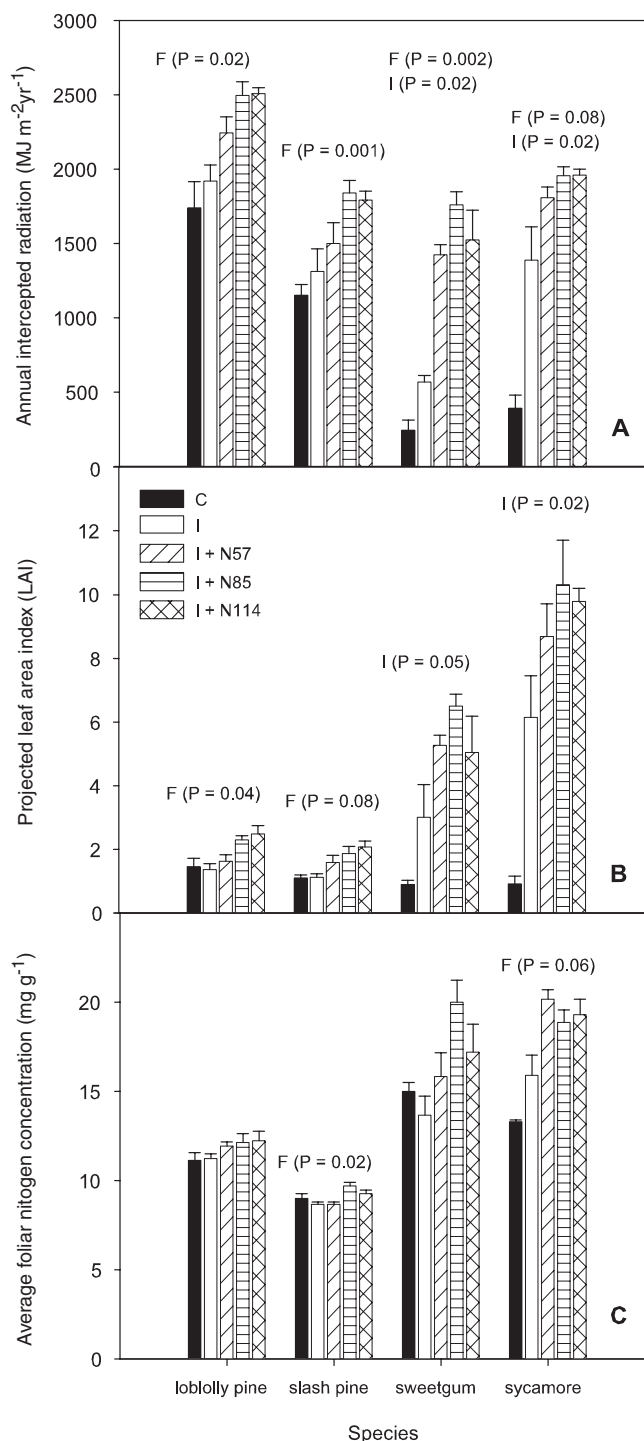


Figure 2—Annual intercepted radiation (A), projected LAI (B), and average foliar nitrogen concentration (C) for the 2001 (fifth) growing season. Treatment codes represent: C = control; I = 3.05 cm water week⁻¹; I + N57 = 3.05 cm water week⁻¹ + 57 kg N ha⁻¹ year⁻¹; I + N85 = 3.05 cm water week⁻¹ + 85 kg N ha⁻¹ year⁻¹; I + N114 = 3.05 cm water week⁻¹ + 114 kg N ha⁻¹ year⁻¹. F indicates a significant effect of fertilization, I indicates a significant effect of irrigation with P-values in parentheses (bars represent 1 standard error).

affect LAI for either hardwood species, the I + N85 treatment increased LAI by 116 percent and 66 percent for sweetgum and sycamore, respectively. Irrigation increased LAI for hardwood species (sweetgum, 233 percent; syca-

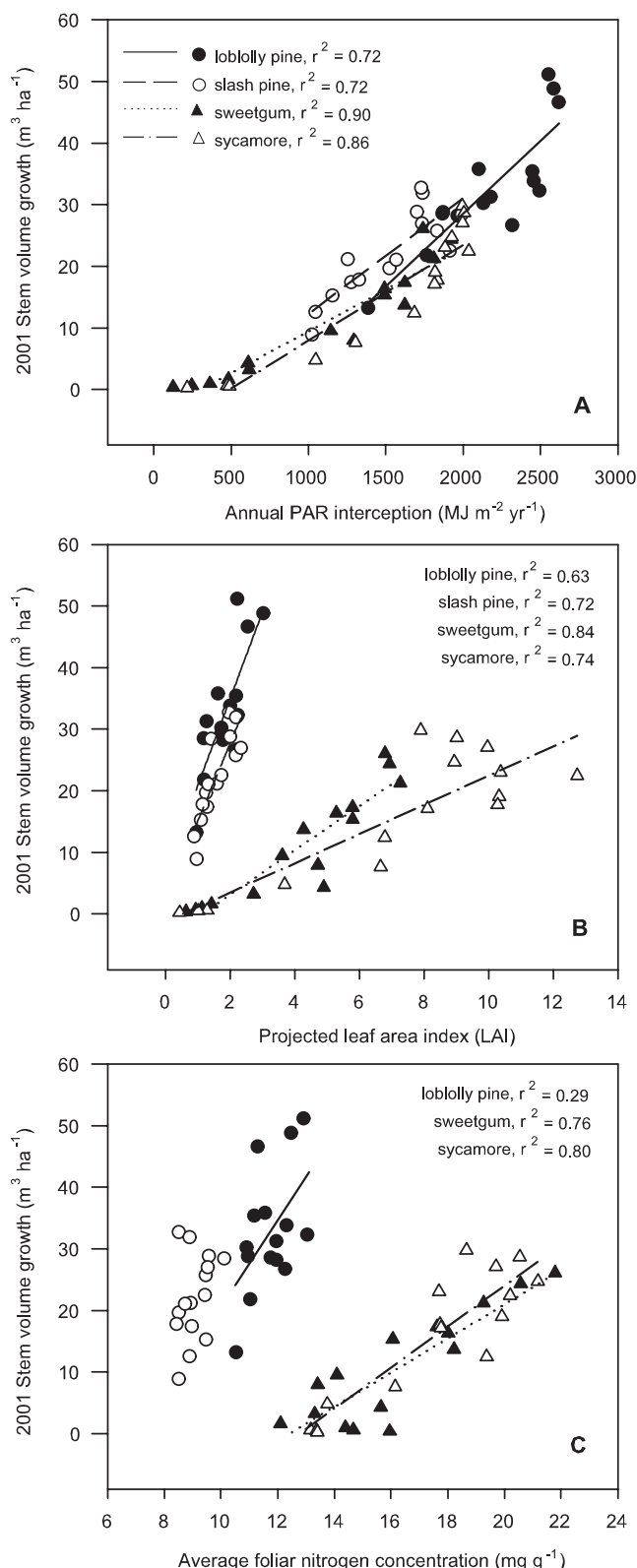


Figure 3—Relationships between 2001 (fifth growing season) stem-volume growth and annual intercepted radiation (A), projected LAI (B), and average foliar nitrogen concentration (C).

more, 589 percent) but did not affect either of the pine species (fig. 2). Good correlations were found between projected LAI and 2001 stem-volume growth for all species (fig. 3). The relationships for hardwood and pine species

were distinct from one another, although this distinction would be less if the 2001 foliage cohort were included in estimates of pine LAI.

Foliar Nitrogen Concentration

Fertilization significantly affected average foliar [N] for slash pine and sycamore whereas irrigation had no significant effects (fig. 2). In the hardwood species, values of [N] were higher and more variable than those of the pines and tended to increase more with fertilization. Average [N] was highly correlated with stem volume growth for sweetgum and sycamore, both of which exhibited similar regression lines (fig. 3). There was a weak correlation between stem-volume growth and [N] for loblolly pine and no statistical relationship for slash pine.

DISCUSSION

Fertilization increased standing volume and volume production during the 2001 growing season. Although there were no significant differences between fertilization treatments, the highest growth occurred at the intermediate fertilization level. This probably indicates that annual application of 85 kg ha^{-1} of N at this point in stand development was meeting nutrient demand and that adding more may have had a negative impact. As the stands continue to grow and take up more nitrogen, the higher levels of nitrogen fertilization may result in additional growth increases. A similar study on *Pinus radiata* (D. Don) (Fife and Nambiar 1997) showed no differences in growth at the two highest levels of fertilization. Hardwood species responded more to application of resources than did pine species. Specifically, sycamore showed the largest gains from irrigation whereas sweetgum benefited the most from fertilization. A short rotation trial in the Coastal Plain of Alabama found similar results—that fertilization increased height and d.b.h. of both sycamore and sweetgum, and irrigation increased these parameters for sycamore only (Lockaby and others 1997).

Increases in canopy size due to resource addition were similar to those for stem growth. As a result, IPAR and LAI were well correlated to stem-volume growth. Many other studies found linear relationships between growth and IPAR (Cannell and others 1987, Dalla-Tea and Jokela 1991, Landsberg and Wright 1989, Linder 1985, Monteith 1977, Will and others 2000) and LAI (Albaugh and others 1998, Samuelson and others 2001). A study on slash pine in Florida, however, found no relationship between IPAR and NPP (Gholz and others 1991).

In this study, it was not possible to determine causal relationships. However, IPAR explained a larger amount of the variation in stem-volume growth than did LAI, possibly indicating that radiation interception may be more important for determining stem growth than photosynthetic surface area. Also, similar relationships between hardwoods and pines for IPAR may indicate a functional relationship between IPAR and growth regardless of genotype or canopy architecture. In contrast, the relationship between LAI and stem growth differed for hardwoods and pines (even if the 2001 cohort was added to estimates of LAI).

Foliar [N] was higher, the range among treatments greater, and the correlation between stem growth and [N] better in

the hardwood stands than in the pine stands. Fertilization usually increases in foliar [N] of pine (Beets and Whitehead 1996, Fife and Nambiar 1997; Jose and others, in press; Maier 2001; Murthy and others 1996). However, the response may depend on inherent site fertility. For instance, a loblolly pine fertilization study in North and South Carolina found elevated foliar [N] with fertilization for only two of three locations (Vose and Allen 1988). The lack of correlation between foliar [N] and growth for the pine species in our study could be due to the small response or use of nitrogen applied as fertilizer by pines for foliar development and other uses (N dilution).

The results obtained in this study indicate that both IPAR and LAI can be useful predictors of stand growth of different species under a wide range of resource availabilities. In this case, foliar nitrogen concentration had good predictive capabilities for hardwood species but not for either of the pine species. The ease of IPAR measurements compared to those for LAI as well as the better correlations make IPAR measurements the best candidate as a predictor of stand growth.

ACKNOWLEDGMENTS

We thank Robert McGarvey for his aid in the collection of data that otherwise would have proven unattainable, as well as Dr. Robert Teskey and Dr. Mark Coleman for their valuable comments on the manuscript. We also thank Plum Creek Timber Company for funding and assistance and the Traditional Industries Program for Pulp and Paper (TIP³) for funding.

LITERATURE CITED

- Albaugh, T.J.; Allen, H.L.; Dougherty, P.M. [and others]. 1998. Leaf area and above- and belowground responses of loblolly pine to nutrient and water additions. *Forest Science*. 44: 317-328.
- Beets, P.N.; Whitehead, D. 1996. Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. *Tree Physiology*. 16: 131-138.
- Cannell, M.G.R.; Milne, R.; Sheppard, L.J.; Unsworth, M.H. 1987. Radiation interception and productivity of willow. *Journal of Applied Ecology*. 24: 261-278.
- Dalla-Tea, F.; Jokela, E.J. 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. *Forest Science*. 37: 1298-1313.
- Fife, D.N.; Nambiar, E.K.S. 1997. Changes in the canopy and growth of *Pinus radiata* in response to nitrogen supply. *Forest Ecology and Management*. 93: 137-152.
- Gholz, H.L.; Vogel, S.A.; Cropper, J., W.P. (and others). 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, North Florida. *Ecological Monographs*. 61: 33-51.
- Gower, S.T.; Vogt, K.A.; Grier, C.C. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. *Ecological Monographs*. 62: 43-65.
- Grace, J.C. 1987. Theoretical ratio between "one-sided" and total surface area for pine needles. *New Zealand Journal of Forestry Science*. 17: 292-296.
- Green, T.H.; Mitchell, R.J.; Gjerstad, D.H. 1994. Effects of nitrogen on the response of loblolly pine to drought II. Biomass allocation and C:N balance. *New Phytologist*. 128: 145-152.
- Jose, S.; Merritt, S.; Ramsey, C.L. [In press]. Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water and nitrogen. *Forest Ecology and Management*.
- Keyes, M.R.; Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research*. 11: 599-605.
- Kuers, K.; Steinbeck, K. 1998. Leaf area dynamics in *Liquidambar styraciflua* saplings: responses to nitrogen fertilization. *Canadian Journal of Forest Research*. 28: 1660-1670.
- Landsberg, J.J.; Wright, L.L. 1989. Comparison among *Populus* clones and intensive culture conditions, using an energy-conversion model. *Forest Ecology and Management*. 27: 129-147.
- Li, C.; Wang, K. [In press]. Differences in drought responses of three contrasting *Eucalyptus microtheca* F. Muell. populations. *Forest Ecology and Management*.
- Linder, S. 1985. Potential and actual production in Australian forest stands. In: Landsberg, J.J.; Parsons, W., eds. Canberra, Australia: Research for Forest Management CSIRO: 11-35.
- Lockaby, B.G.; Clawson, R.G.; Baker, T. 1997. Response of three hardwood species to irrigation and fertilization on an upland site. *Southern Journal of Applied Forestry*. 21: 123-129.
- Maier, C.A. 2001. Stem growth and respiration in loblolly pine plantations differing in soil resource availability. *Tree Physiology*. 21: 1183-1193.
- Maier, C.A.; Johnsen, K.H.; Butnor, J. [and others]. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization. *Tree Physiology*. 22: 1093-1106.
- McMurtrie, R.E.; Benson, M.L.; Linder, S. [and others]. 1990. Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. *Forest Ecology and Management*. 30: 415-423.
- Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London*. 281: 277-294.
- Munger, G.T.; Will, R.E.; Borders, B.E. [In press]. Effects of competition control and annual nitrogen fertilization on gas exchange of different aged *Pinus taeda*. *Canadian Journal of Forest Research*.
- Murthy, R.; Dougherty, P.M.; Zarnoch, S.J.; Allen, H.L. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. *Tree Physiology*. 16: 537-546.
- Nelson, L.E.; Shelton, M.G.; Switzer, G.L. 1995. Aboveground net primary productivity and nutrient content of fertilized plantation sweetgum. *Soil Science Society of America Journal*. 59: 925-932.
- Osorio, J.; Osorio, M.L.; Chavez, M.M.; Pereira, J.S. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology*. 18: 363-373.
- Sampson, D.A.; Allen, H.L. 1998. Light attenuation in a 14-year-old loblolly pine stand as influenced by fertilization and irrigation. *Trees*. 13: 80-87.
- Samuelson, L.J. 1998. Influence of intensive culture on leaf net photosynthesis and growth of sweetgum and loblolly pine seedlings. *Forest Science*. 44: 308-316.
- Samuelson, L.J. 2000. Effect of nitrogen on leaf physiology and growth of different families of loblolly and slash pine. *New Forests*. 19: 95-107.
- Samuelson, L.J.; Stokes, T.; Cooksey, T. [and others]. 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. *Tree Physiology*. 21: 369-376.
- Vose, J.M.; Allen, H.L. 1988. Leaf area, stemwood growth, and nutrient relationships in loblolly pine. *Forest Science*. 34: 547-563.
- Wendler, R.; Millard, P. 1996. Impacts of water and nitrogen supplies on the physiology, leaf demography and nitrogen dynamics of *Betula pendula*. *Tree Physiology*. 16: 153-159.
- Will, R.E.; Barron, G.A.; Burkes, E.C. [and others]. 2000. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. *Forest Ecology and Management*. 154: 155-163.